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VARIATION IN SONG RATE DURING THE BREEDING CYCLE OF THE RUFOUS BUSH CHAT, *CERCOTRICHAS GALACTOTES*

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SUMMARY.—*Variation in song rate during the breeding cycle of the Rufous Bush Chat* Cercotrichas galactotes. This study is an attempt to elucidate the functions of song in the Rufous Bush Chat *Cercotrichas galactotes*, mainly in relation to the temporal pattern of song production during the stages of the reproductive cycle. Territorial males sing at the highest rate during the period of territory establishment and pair formation, declining to a lower level during the fertile period of the mate and remaining at a low (but partially higher) level afterwards. This result, together with the observation of a constant high rate of song produced by a male which lost his mate, support the mate-acquisition and territory-establishment hypotheses on the functions of song, and suggests that the decrease during the fertile period of the mate may represent an attempt by the males to hide the fertility status of their mates from potential male competitors. The partial increase in song rate during the neighbouring females' fertile periods suggests an EPCs seeking function. Males do not adjust their singing rate to avoid detection of nest during the time of potential brood parasitism by the Cuckoo *Cuculus canorus*, and they sing much less during the period of nest occupancy, in this way perhaps eluding nest detection by potential predators.

Key words: Breeding stages, *Cercotrichas galactotes*, mate-acquisition, song, territory-establishment.

RESUMEN.—*Variación en la tasa de canto durante el ciclo reproductivo en el Alzacola* Cercotrichas galactotes. Este estudio intenta aclarar las funciones del canto en el Alzacola *Cercotrichas galactotes*, principalmente en relación con el modelo temporal de las tasas de canto durante las fases del ciclo reproductivo. Los machos territoriales cantan con tasa máxima durante el periodo de establecimiento del territorio y formación de pareja, disminuyendo a un nivel inferior durante el periodo fértil de la pareja y permaneciendo a un nivel inferior (aunque parcialmente algo más alto) en las fases reproductivas posteriores. Este resultado, junto con la observación del nivel alto y constante de canto de un macho que perdió a su pareja, apoyan la hipótesis de las funciones del canto en la adquisición de pareja y en el establecimiento del territorio, sugiriendo además que el modelo de producción de canto puede estar ayudando a ocultar el periodo fértil de la hembra respecto a posibles machos competidores. El aumento parcial de las tasas de canto durante el periodo fértil de la hembras vecinas sugiere una función de obtención de cópulas con dichas hembras. Los machos no ajustan su tasa de canto para evitar la detección del nido en el tiempo de parasitismo potencial por el Cuco *Cuculus canorus*, aunque sí lo hacen, cantanto mucho menos, durante el periodo de ocupación del nido, de esta forma quizá eludiendo la detección del mismo por posibles predadores.

Palabras claves: Adquisición de pareja, canto, *Cercotrichas galactotes*, establecimiento del territorio, fases reproductivas.

INTRODUCTION

Under the general functions of songs of territorial male passerines repelling rival males and attracting females, the roles of establishment and maintenance of breeding territories and the acquisition and defence of female mates are the most widely recognized (Krebs, 1976, 1977; Catchpole, 1979; Greig-Smith, 1982a; Searcy & Andersson, 1986).

In relation to the function of song helping to keep-out potential intruders during the fertile period of the mate, the announcement of its fertility status by singing has been interpreted as a form of mate guarding (Møller, 1988, 1991). On the other hand, the decreasing level of song activity observed in other male passerines during their mates' fertile period suggests that hiding their fertility status from potential male competitors may be

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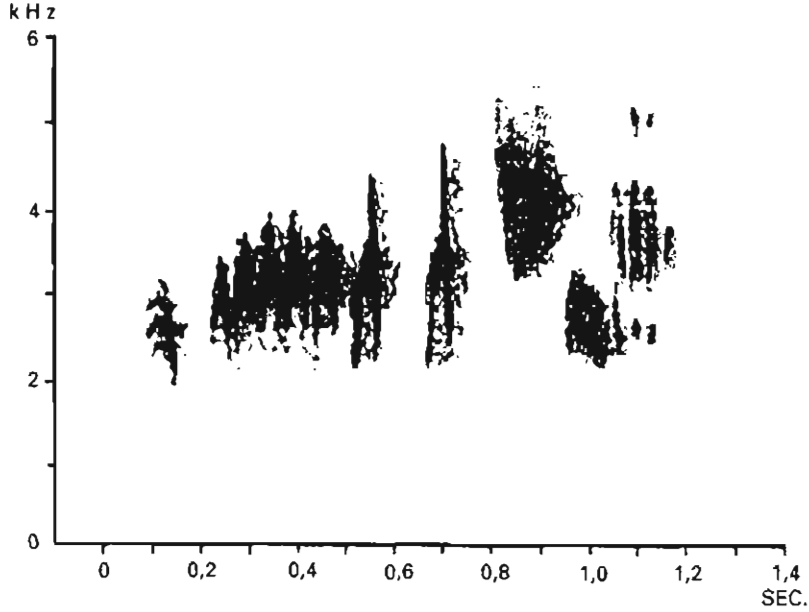

FIG 1.—Sonagram of a typical territorial song recorded at the study area.
[Sonograma de un canto territorial típico registrado en el área de estudio.]

an alternate strategy (Armstrong, 1973; Lampe & Espmark, 1987; Hanski & Laurila, 1993).

Under the sperm competition hypothesis, another recognized function of song (besides that of mate guarding) may be to help the male singer to obtain extra-pair copulations (EPCs) by attracting neighbouring females (Greig-Smith, 1982a; Møller, 1991).

I shall approach this topic in the Rufous Bush Chat *Cercotrichas galactotes* by considering the timing of song and the distance of song posts to the nests locations in relation to the phases of the nesting cycle and to the mates' and neighbouring females' fertile periods.

As Rufous Bush Chats are heavily parasitized and preyed upon by the Cuckoo *Cuculus canorus* in the area of study (Alvarez, 1994a,b) and song may provide cues to the location of nests, Y shall also try to elucidate whether the males' singing rate is adapted to elude brood parasitism and/or nest predation.

STUDY AREA AND METHODS

The study area (19 ha in 1992, extended to 25 ha in 1993), 20 km to the southeast of Seville, Spain, is mostly dedicated to intensive vineyard agriculture with interspersed fruit trees and small patches of kitchen gardens.

The study was undertaken during two reproductive seasons and extended from the beginning of May to the middle of september (before Rufous Bush Chats started breeding and after most adults had left the area, Alvarez, pers. obs.). The area was inspected every one or two days, looking for new nests of Rufous Bush Chats and monitoring those in progress.

Trapping was undertaken as birds were arriving to the study area and all the territorial individuals present (20 males and 21 females) were captured (with mist nets and baited traps) and colour ringed. Mate guarding is not an apparent male strategy of the population studied, both sexes are involved in

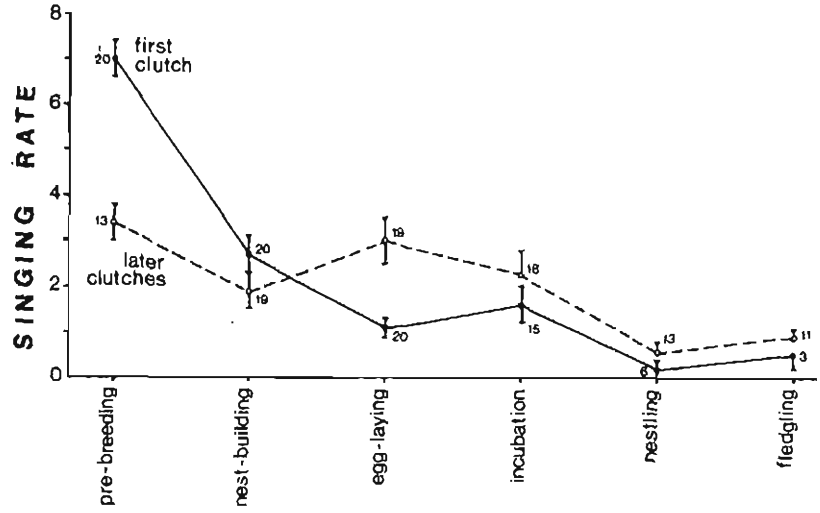

FIG 2.—Average singing rate (±s.e.) of male Rufous Bush Chats through the phases of the nesting cycle. Data are combined from 20 and 27 complete and incomplete first and later cycles, respectively, of 10 pairs in 1992 and 9 pairs and a trio in 1993. Sample size (number of pairs) is indicated near each value (variation in this respect results mainly from predation upon nests and the start of nest-building immediately after nest predation, without an interval of pre-breeding betwen cycles).
[Tasa media de canto (±s.e.) de machos de Alzacola durante las fases del ciclo reproductivo. Los datos proceden de la combinación de la información obtenida a partir de 20 nidadas completadas y 27 incompletas de 10 parejas nidificantes en 1992 y 9 parejas y un trío en 1993. El tamaño de la muestra (número de parejas) se indica junto a cada valor, procediendo su variación principalmente de la predación sobre los nidos y del comienzo en algunos casos de la fase de construcción de nido inmediatamente después de haber sido predado el nido anterior, sin darse una fase pre-reproductiva entre ciclos.]

nest-building and while males are readily observed while singing and patrolling their territories, the silent and secretive behaviour of the females before the time of chick feeding renders them almost unobservable (Alvarez, pers. obs.).

The song of the Rufous Bush Chat is a repetition of discrete song-phrases (a sonagram of a typical territorial song, recorded in the study area, is presented in Fig. 1). In order to obtain a measure of individual singing rate, I walked a fixed route (from which the whole study area could be seen) 10 times (every half hour) every two days, starting at 0600 DST. The identity of each singer was registered the first time that an individually recognized Rufous Bush Chat was observed in each of the 10 walks along the fixed route (thus individual daily singing rate could vary between 0 and 10), as well as its position onto a scale map (scale 1:1,000) of the study area.

The phases of the breeding cycle considered were: a) pre-breeding: from the bird's first sighting or after end of previous clutch, until the 6th day prior to egg-laying; this phase does not always occur for second or replacement clutches, b) nest-building: from 5th day before egg-laying, usual start of nest-building, to day before start of egg-laying, and c) egg-laying, d) incubation, e) nestling and f) fledgling.

Following Birkhead & Møller (1992), I designated the fertile period of the females as beginning five days prior to the laying of the first egg and ending the day of laying the penultimate egg. The females considered in this respect for each male were his own mate and the female occupying the nearest territory.

The time of potential brood parasitism by the Cuckoo was considered to be from the second day of egg-laying to the second day of

TABLE 1

Singing rate (mean ± SD) and result of comparisons of individual mean singing rates during the presumed female mates' pre-fertile, fertile and post-fertile periods.
[Tasa de canto (media ± DE) y resultado de las comparaciones de tasas medias individuales durante los periodos pre-fértil, fértil y post-fértil de las hembras con que los machos estaban emparejados.]

Study period	*Pre-fertile*	*Fertile*	*Post-fertile*	*n*
1992*	5.8 ± 1.9	2.3 ± 1.1	1.5 ± 0.8	10
1993** ...	4.6 ± 1.9	2.3 ± 1.2	1.6 ± 1.5	9

* $\chi^2 = 13.40$, df = 2, $P = 0.00003$ (Friedman test).
** $\chi^2 = 14.89$, df = 2, $P = 0.00005$ (Friedman test).

incubation (Alvarez, pers. obs.) and the time of potential nest predation was that of nest occupancy (combined laying, incubation and nestling periods).

RESULTS

Singing rate was at the highest during territory establishment (pre-breeding of the first cycle: 1992: $\bar{x} = 7.3$, SD = 1.2, $n = 10$; 1993: $\bar{x} = 6.3$, SD = 2.2, $n = 10$), declining to a significant lower level during nest-building (1992: $\bar{x} = 2.6$, SD = 1.4, $n = 10$, $t = 0$, $P < 0.01$; 1993: $\bar{x} = 2.5$, SD = 1.9, $n = 10$, $t = 0$, $P < 0.01$, Wilcoxon test), and remaining low during the next phases of the first and subsequent clutches (Fig. 2, for both years combined).

When considering the pattern of fertility variation in time, the males' singing rate during their mates' fertile period was lower than that during the pre-fertile period (1992: $t = 1$, $n = 10$, $P < 0.01$; 1993: $t = 0$, $n = 9$, $P = 0.01$; Wilcoxon test) and, when compared with the rate during the post-fertile period (last day of egg-laying plus the incubation period for those males whose mates reached the latter stage at some time of their breeding cycles) the rate was not statistically different for 1992 ($t = 10$, $n = 10$, $P > 0.05$; Wilcoxon test) and it was significantly higher for 1993 ($t = 3$, $n = 9$, $P < 0.05$; Wilcoxon test) (Table 1).

When considering the singing rate not for the whole fertile period, but dividing it into their nest-building and egg-laying components, no significant difference was found in the comparison of the rates during these two components (Table 2).

Nevertheless, when the potential effect of early season (period of territory establishment and pair formation) on the singing rate was eliminated by excluding from the analysis the data related to the periods of nest-building and egg-laying of the first nest, the rate during nest-building was lower than that during the subsequent egg-laying, although only significantly so during 1992 (Table 2).

TABLE 2

Singing rate (mean ± SD) during the nest-building and egg-laying periods for a) the whole reproductive period of each pair and b) excluding the nest built immediatly after territory establishment and pair formation.
[Tasa de canto (media ± DE) durante los periodos de construcción de nido y de puesta durante a) todo el periodo reproductivo y b) excluyendo el nido construído inmediatamente tras el establecimiento del territorio y la formación de la pareja.]

	*Wwhole reproductive period**			*Excluding first nest***		
Study period	*Nest-building*	*Egg-laying*	*n*	*Nest-building*	*Egg-laying*	*n*
1992	2.8 ± 3.1	2.3 ± 1.4	10	1.8 ± 1.8	3.3 ± 2.0	9
1993	2.3 ± 1.3	1.8 ± 1.7	10	2.2 ± 1.6	2.6 ± 2.2	10

* 1992: $t = 13$, $n = 8$, $P > 0.05$; 1993: $t = 16$, $n = 9$, $P > 0.05$ (Wilcoxon test).
** 1992: $t = 3.5$, $n = 8$, $P < 0.05$; 1993: $t = 8$, $n = 8$, $P > 0.05$ (Wilcoxon test).

TABLE 3

Singing rate (mean ± SD) of a male that lost his mate (male H) and of the seven mated males coinciding with him in the study area (B, C, D, G, I, K, O), and results of comparisons of individual singing rates (Friedman test*) and of comparisons of male H's singing rate with those of the mated males (Wilcoxon test), from the day after losing the mate to his last day of stay (comparisons made of individual rates registered the same day)

[Tasa de canto (media ± DE) del macho que perdió su pareja (macho H) y de los siete machos emparejados que coincidieron con él en el área de estudio (B, C, D, G, I, K, O) y resultados de comparación de conjunto de tasas individuales (test de Friedman) y de la comparación de la tasa de canto del macho H con las de los machos emparejados (test de Wilcoxon), desde el día siguiente a perder la hembra hasta el último día de la estancia de este macho (las comparaciones se hicieron entre las tasas registradas en el mismo día.]*

			T	*n*	*P*
Unmated male*	H	6.6 ± 2.7		18	
Mated males	B	0.9 ± 1.5	0	18	<0.01
	C	0.7 ± 1.3	0	18	<0.01
	D	3.8 ± 2.7	15.5	18	<0.01
	G	1.0 ± 1.3	0	18	<0.01
	I	0.7 ± 0.0	0	18	<0.01
	K	1.1 ± 1.9	0	18	<0.01
	O	1.6 ± 1.3	17.0	17	<0.01

* $\chi^2 = 58.90$, df = 7, P = (Friedman test).

A case of potential interest may be that of a male which lost his mate about half way of reproduction in 1993 (she was found injured during the egg-laying phase and all nesting activity stopped afterwards, only the male remaining in the territory). The singing rate of this male during the period after losing his mate was significantly higher than the rates of the seven mated males coinciding with him in the study area until his last day of stay (Table 3).

In relation to the fertility status of the nearest neighbour females, the data about the males' singing rates departed from random only in 1992, when the mean rate during the fertile period was not different from that during the pre-fertile period ($t = 20$, $n = 10$, $P > 0.05$; Wilcoxon test), although it was significantly higher than the rate during their post-fertile period ($t = 3$, $n = 9$, $P < 0.05$; Wilcoxon test) (Table 4).

The singing rate during the period of potential brood parasitism by the Cuckoo was not lower or higher than either that during the remainder of the incubation period (for the males' clutches in which egg-laying was followed by incubation) or than that during the previous period (from the fifth day before egg-laying to the first day of egg-laying) (Table 5).

On the other hand, the singing rate during the time of potential nest predation (period of nest occupancy) was significantly lower than that during the previous period (1992: nest occupancy: $\bar{x} = 1.1$, SD = 0.6; previous period:

TABLE 4

Singing rate (mean ± SD) and results of comparisons of individual mean singing rates during the fertile, pre-fertile and post-fertile periods of females of neighbouring territories.

[Tasa de canto (media ± DE) y resultado de las comparaciones de tasas medias individuales durante los periodos fértil, pre-fértil y post-fértil de las hembras de territorios vecinos.]

	Fertile	*Pre-fertile*	*Post-fertile*	*n*
1992*	4.0 ± 2.8	3.6 ± 1.9	1.8 ± 1.4	10
1993**	2.8 ± 1.4	3.1 ± 1.7	1.9 ± 1.2	9

* $\chi^2 = 6.20$, df = 2, $P = 0.045$ (Friedman test).
** $\chi^2 = 4.22$, df = 2, $P = 0.12$ (Friedman test).

TABLE 5

Singing rate (mean ± SD) and results of comparisons of individual singing rates during the period of potential brood parasitism by the Cuckoo, during the previous period and during the remainder of the incubation period.
[Tasa de canto (media ± DE) y resultado de las comparaciones de tasas medias individuales durante el periodo de posible parasitismo reproductivo por el Cuco, durante el periodo anterior y durante el resto del periodo de incubación.]

	Potential brood parasitism	*Previous*	*Remainder of incubation*	*n*
1992*	2.2 ± 1.3	2.2 ± 1.6	1.5 ± 0.9	9
1993**	2.6 ± 2.0	2.1 ± 1.6	2.9 ± 1.6	8

* $\chi^2 = 1.65$, df = 2, $P = 0.44$ (Friedman test).
** $\chi^2 = 0.28$, df = 2, $P = 0.87$ (Friedman test).

$\bar{x} = 4.3$, SD = 1.8; following period: $\bar{x} = 2.2$, SD = 1.6; $\chi^2 = 11.40$, df = 2, $P = 0.00008$ (Friedman test); $t = 1$, $n = 10$, $P < 0.01$; 1993: nest occupancy: $\bar{x} = 1.7$, SD = 1.0; previous period: $\bar{x} = 3.5$, SD = 1.2; following period: $\bar{x} = 1.8$, SD = 1.1; $\chi^2 = 15.00$, df = 2, $P = 0.00005$ (Friedman test); $t = 0$, $n = 10$, $P < 0.01$; Wilcoxon test), but only partially different than the rate for the following period (1992: $t = 5$, $n = 10$, $P < 0.05$; 1993: $t = 25$, $n = 10$, $P > 0.05$; Wilcoxon test).

In relation to the location of song posts, their distance to each nest's location during the female mates' fertile periods was lower than that during their post-fertile periods (1992: fertile: $\bar{x} = 36.0$ m, SD = 19.7 m, $n = 9$; post-fertile: $\bar{x} = 46.2$ m, SD = 21.1 m, $n = 9$; $t = 0$, $P < 0.01$; 1993: fertile: $\bar{x} = 52.7$ m, SD = 19.4 m, $n = 10$; post-fertile: $\bar{x} = 77.1$ m, SD = 40.0 m, $n = 10$; $t = 2$, $P < 0.01$; Wilcoxon test).

When the nest-building and egg-laying components of the mates' fertile periods were considered separately, the average distance from song posts to nest was lower in the former period, although the difference was only partially significant (1992: nest-building: $\bar{x} = 27.4$ m, SD = 16.1 m, $n = 9$; egg-laying: $\bar{x} = 30.3$ m, SD = 16.0 m, $n = 9$; $t = 3$, $n = 9$, $P < 0.05$; 1993: nest-building: $\bar{x} = 44.0$ m, SD = 20.5 m, $n = 10$; egg-laying: $\bar{x} = 45.1$ m, SD = 17.7 m, $n = 10$; $t = 11$, $n = 8$, $P > 0.05$; Wilcoxon test).

DISCUSSION

The high level of song activity in early season suggests that the song of male Rufous Bush Chats serves to establish territorries and/or to acquire mates, two non-exclusive and widely extended roles of passerine song, as shown in field (Catchpole, 1979; Greig-Smith,1982a; Searcy & Andersson, 1986) and laboratory studies (McDonald, 1989; Eens *et al.*, 1990).

The mate-acquisition role of song production is supported by the finding of a high level of song by the individual which lost his mate when the breeding cycle was well advanced, in any event, the hypothesis of joint territory-establishment and mate-acquisition functions remains unimpaired. Reports of high song level in unmated, non-breeding males or in males after losing their mates in other bird species are not rare (Catchpole, 1973; Greig-Smith 1982b; Hanski & Laurila, 1993).

A high level of song activity in early season and a depression after pairing are apparently common in passerines (Catchpole, 1973; Lampe & Espmark, 1987; Björklund *et al.*, 1989; Hanski & Laurila, 1993), suggesting a wide extent of the mate-acquisition and perhaps also of the territory-establishment role. Furthermore, some experimental evidence (e.g. increase in the time spent singing after introduction of a female for the European Starling *Sturnus vulgaris*, Eens *et al.*, 1990; and attraction of mates by male Scott's Seaside Sparrows *Ammodramus maritimus* after being mateless while temporarily muted, McDonald, 1989) also support the mate-acquisition hypothesis.

While the function of song attracting female mates appears as very likely for Rufous Bush Chats, the way how female choice for constant male singers has evolved is less clear. Since the birds of the population studied apparently do not obtain a significant amount of food from the breeding territories, if females would use singing rate as an indication of male quality, the rate should be related to

other aspects not investigated in the present study (as it does with provisioning of young and nest defence in the Stonechat *Saxicola torquata*, Greig-Smith, 1982b).

We can visualize song rate as an indication of phenopytic quality (and overall genetic constitution, Andersson, 1986) resulting of the apparently high cost of singing and its incompatibility with food searching activities. In connection with this, the evidence available in passerines concerns the high cost of singing (as measured by oxygen consumption) in the Carolina Wren *Thryothorus ludovicianus* (Eberhardt, 1994) and the experimentally induced high song rates when birds are provided with supplemented food (Searcy, 1979; Wilhelm *et al.*, 1982; Pflumm *et al.*, 1984; Gottlander, 1987; Reid, 1987; Strain & Mumme, 1988) and by the direct relationship of song rate to ambient or overnight temperature (Curio, 1959; Garson & Hunter, 1979; Higgins, 1979; Gottlander, 1987; Reid, 1987; Santee & Bakken, 1987; Strain & Mumme, 1988).

As depletion of energy reserves might threaten survival, only vigorous males (with still abundant energy reserves) would go on singing, instead of turning to foraging, so providing the female with a reliable indication of good phenotypic condition. This hypothesis is applicable to Rufous Bush Chat males, whose singing behaviour (they sing from high song posts) is wholy incompatible with foraging (they search for food at or near ground level).

The decrease in the rate of song observed during the mates' fertile period indicates that male Rufous Bush Chats have not adopted the strategy of fertility announcement (Møller, 1988, 1991), but they rather may be trying to hide the fertility status of the mate from potential male competitors.

As males were registered singing nearer the nest's location during the fertile period of the mate, we can provisionally visualize the situation as an equilibrium between the needs to keep the fertility status of the mate secret and to defend either the mate or the nest.

In fact, the nest-building activities may have an influence on the rate of song (by subtracting time allocated to it), as suggested by the lower rate registered during the nest-building component of the mates' fertile period. In any event, the persistence of a relatively low rate of song during the egg-laying component of the fertile period suggests that the role of fertility-hiding may be at work.

The decrease of the level of song production observed in other singing passerines during their mates' fertile periods (Armstrong, 1973; Lampe & Espmark, 1987; Hanski & Laurila, 1993) suggests that hiding the mate's fertility status from potential male competitirs is not uncommon.

Furthermore, the slight adjustment observed of the song rate of male Rufous Bush Chats to the breeding cycles of neighbouring females during one of the two years of study (higher rates during their fertile periods, as compared to post-fertile) suggests that singing males could also be seeking extra-pair copulations, as it is apparently the case also for the Stonechat (Greig-Smith, 1982a). The observation of a trio of one male and two females in the study area in 1993 (both females keeping their own nest in the male's territory) suggests that singing males could perhaps be trying to obtain a second female.

On the other hand, the results allow us to discard a potential adaptation of the temporal pattern of song production helping to elude brood parasitism in the Rufous Bush Chat, while a function of eluding nest detection during the period of nest occupancy (and therefore helping to reduce nest predation) should be taken into consideration.

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